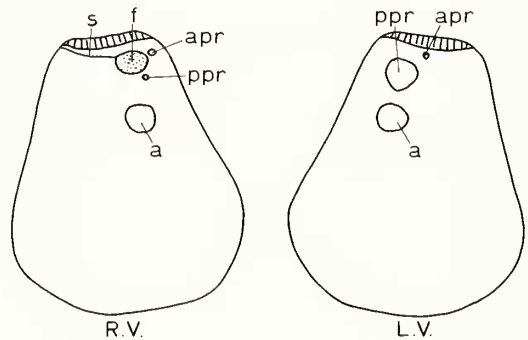


REVISION OF THE BIVALVE FAMILY PULVINITIDAE STEPHENSON, 1941

by T. J. PALMER

ABSTRACT. Reconsideration of the characteristics of all species referred to the three genera which have hitherto constituted the Family Pulvinitidae Stephenson, 1941, indicates that all should be accommodated in the nominate genus, *Pulvinites* Blainville, 1824. A new species, *P. mackerrowi* from the middle Jurassic of England (the earliest known representative of the family) is described.

THE bivalve family Pulvinitidae Stephenson, 1941, comprises a small, poorly known taxon with a discontinuous stratigraphic range from the Jurassic to the Recent. It appears to represent an offshoot of the Family Isognomonidae whose byssus has become enclosed by growth together of the dorsal and ventral margins of the right byssal notch (Cox 1969). The byssus thus appears, as in *Anomia*, to pass through a hole in the right valve. This hole is connected to the antero-dorsal shell margin by a suture (text-fig. 1).



TEXT-FIG. 1. Diagrammatic representation of the features observable on the inner surfaces of the valves of all species of the genus *Pulvinites*. s = suture; f = byssal foramen; a = adductor muscle scar; apr = anterior pedal retractor muscle scar; ppr = posterior pedal retractor muscle scar.

CONSTITUENT GENERA OF THE FAMILY PULVINITIDAE

The family was erected without a formal diagnosis by Stephenson (1941) as a repository for the best-known genus, *Pulvinites* Blainville, 1824. Species of this genus have been described from a number of upper Cretaceous localities in North America (Conrad 1858, 1860; Wade 1926; Stephenson 1914, 1926, 1941), Lebanon (Vokes 1941), and Antarctica (Zinsmeister 1978), and from the Palaeocene of California (Zinsmeister 1978). The American occurrences include exceptionally well-preserved material from the Maastrichtian Ripley Formation of Coon Creek, Tennessee. The only known occurrence in the European Cretaceous is that of the type material of *P. adansonii* Blainville, 1824, from the Maastrichtian Calcaire à Baculites (Craie de Valognes) at Frésville in the Cotentin peninsula, France.

Two other genera have hitherto been placed in the family (Cox 1969): *Hypotrema* d'Orbigny, 1853 from the French upper Jurassic and the extant *Foramulina* Hedley, 1914 from south-east Australia. The wide geographic and stratigraphic distribution of the three genera has led to confusion about their similarities and differences. The authors of many of the species, as well as of the later two genera, have suffered from inaccessibility to, and unfamiliarity with, appropriate comparative material from

the related taxa, and have been unable to gain a correct impression of the true characteristics and considerable variability of members of this family. As a result many misconceptions are stated in the literature, and the family is taxonomically over-split. Several workers (e.g. Bronn 1852, Stoliczka 1871, Freneix 1956) have claimed or suspected this state of affairs without the information to back their suspicions, but this is the first time that all the species in the family have been studied together. Their characteristics are summarized in Table 1.

MATERIAL STUDIED

Extensive material from all three above-mentioned genera has been examined. It includes the only known surviving specimens of *P. adansonii*, which are topotypes belonging to the de Gerville collection in the British Museum (Natural History); well-preserved topotypes of *P. argenteus* Conrad, 1858 from the Ripley Formation of Tennessee; the type suites of *H. rupellensis* d'Orbigny, 1853 and *H. triangularis* d'Orbigny, 1853 from the d'Orbigny collection in the Museum National d'Histoire Naturelle, Paris; additional topotypes of *H. rupellensis* in the Museum d'Histoire Naturelle at La Rochelle and in the Oxford University Museum (author's collection); the figured paratype of *F. exempla* Hedley, 1914; and one specimen from a recently discovered population of *F. exempla* (the only known soft-part occurrence other than the holotype).

SYSTEMATIC PALAEOLOGY

- Class BIVALVIA Linné, 1758
- Subclass PTERIOMORPHIA Beurlen, 1944
- Order PTERIOIDA Newell, 1965
- Suborder PTERIINA Newell, 1965
- Superfamily PTERIACEA Gray, 1847
- Family PULVINITIDAE Stephenson, 1941

Diagnosis. Shell ovate, orbicular or trigonal; externally lamellose and oyster-like; outer ostracum of prismatic calcite, inner ostracum nacreous; LV usually more inflated than RV, which is often planar or concave; hinge anterior to umbo, edentulous, but with wide ligamental area in each valve bearing series of narrow, elongate, sub-parallel, transverse ligamental pits which indent lower margin of area and which may become lachrymate in some species; RV of post-juvenile has byssal foramen just below middle of ligamental area, joined to antero-dorsal shell margin by suture representing line of ontogenetic closure of byssal notch; LV with enlarged posterior byssal retractor muscle scar opposite foramen; single adductor muscle scars located medially in each valve.

Discussion. Stephenson (1941) gave no diagnosis or description of the family when he erected it as a repository for the genus *Pulvinites*. Cox's (1969) definition of the family gave undue significance to the radial striation of the byssal retractor, which is only seen in some specimens. The above redefinition also excludes those characteristics such as size and convexity considered to be of only subsidiary importance, but includes shell structure.

Much unnecessary doubt has been thrown on the existence of the suture in fossil forms. Cox (1969) states that it has not been observed at all, and Zinsmeister (1978) states that it has not been observed in *P. argenteus*. Conrad (1858, 1867), however, clearly states that it is present in *P. argenteus*, and his figure (Conrad 1860) shows it. He also understood its significance and records (Conrad 1867) that juveniles of that species can be found in which the byssal notch is still open to the anterior. A suture is obvious in all specimens of *P. argenteus* examined in this study. Similarly, the suture is clearly shown in Sowerby's (1833) picture of the topotype of *P. adansonii* (BMNH L63618), and in the specimen itself. All the other right valves in the material examined in this study (see above) also clearly show the suture.

TABLE 1. Morphological characteristics and measurements of all species of the genus *Pulvinites*; junior synonyms in parentheses. Under lateral profile, O = oval; T = trigonal; st, conc, and conv = straight, concave, and convex posterior dorsal margin respectively.

Species; synonyms in inverted commas	Lateral profile	Inflation weak, moderate, or strong	Max. length (l) mm	Max. height (h) mm	l >, =, or < h	Length of ligament mm	Number of ligament pits	Length of ligament mm	Length of ligament mm	Age	Geographic occurrence
<i>adansonii</i>	T, st-conc	weak	53	46	l ≥ h	6-9	7-8	0.9-1.2	4.4-6.3	Maastrichtian	Frésville, Manche, Normandy
'auriculatus'	T conc	weak	51	47	l ≥ h	—	6	—	—	Cenomanian	Hajula, Lebanon
'antarctica'	O, T conc	weak	52	49	l > h	10-11	9-11	1.0-1.1	4.3-5.2	U. Campanian or Maastrichtian	Seymour Is., Antarctica
<i>argenteus</i>	T conv, O, st or conc	weak- mod.	53	52	l >, = or < h	9-15	10-15	0.9-1.0	2.9-3.9	Maastrichtian	Texas, Mississippi, Tennessee, Alabama nr. La Rochelle,
<i>rupellensis</i>	O-oval	mod.- strong	30	50	l < h	5-11	5-12	0.8-1.5	2.1-5.4	Kimmeridgian	Charente Maritime nr. La Rochelle,
'triangularis'	oval w. dorsal taper	mod.	—	—	l < h	8	6	1.3	—	Kimmeridgian	nr. La Rochelle,
<i>mackerrowi</i>	O	strong	30	31	l = h	6-11	6-12	0.8-1.0	2.7-3.8	M. and U. Bathonian	Charente Maritime Oxfordshire
<i>californica</i>	O, T st	weak	18.5	20	l ≤ h	3-5	5	0.7	4-6	uppermost Palaeocene	Ventura Co., California
<i>pacifica</i>	? O	weak	39	44	l < h	—	c.5	—	—	Palaeocene	Ventura Co., California
<i>exempla</i>	T conc	weak	131	111	l > h	36	20	1.8	3-7	Recent	California Gabo Is. Victoria, Aus.

TABLE 1. Morphological characteristics and measurements of all species of the genus *Pulvinites*; junior synonyms in parentheses. Under lateral profile, O = oval; T = trigonal; st. conc. and conv = straight, concave, and convex posterior dorsal margin respectively.

Species; synonyms in inverted commas	Lateral profile	Inflation weak, moderate, or strong	Max. length (l) mm	Max. height (h) mm	l >, =, or < h	Length of ligament mm	Number of ligament pits	Length		Age	Geographic occurrence
								No. of pits	Length of ligament		
<i>adansonii</i>	T, st-conc	weak	53	46	l ≥ h	6-9	7-8	0.9-1.2	4.4-6.3	Maastrichtian	Fréville, Manche, Normandy
' <i>auriculus</i> '	T conc	weak	51	47	l ≥ h	—	6	—	—	Cenomanian	Hajula, Lebanon
' <i>antarctica</i> '	O, T conc	weak	52	49	l > h	10-11	9-11	1.0-1.1	4.3-5.2	U. Campanian or Maastrichtian	Seymour Is., Antarctica
<i>argenteus</i>	T conv, O, st or conc	weak- mod.	53	52	l >, = or < h	9-15	10-15	0.9-1.0	2.9-3.9	Maastrichtian	Texas, Mississippi, Tennessee, Alabama
<i>rupellensis</i>	O-oval	mod. strong	30	50	l < h	5-11	5-12	0.8-1.5	2.1-5.4	Kimmeridgian	nr. La Rochelle, Charente Maritime
' <i>triangularis</i> '	oval w. dorsal taper	mod.	—	—	l < h	8	6	1.3	—	Kimmeridgian	nr. La Rochelle, Charente Maritime
<i>mackerrowi</i>	O	strong	30	31	l ≥ h	6-11	6-12	0.8-1.0	2.7-3.8	M. and U. Bathonian	Oxfordshire
<i>californica</i>	O, T st	weak	18.5	20	l ≤ h	3.5	5	0.7	4.6	uppermost Palaeocene	Ventura Co., California
<i>pacifica</i>	? O	weak	39	44	l < h	—	c.5	—	—	Palaeocene	Ventura Co., California
<i>exempla</i>	T conc	weak	131	111	l > h	36	20	1.8	3.7	Recent	Gabo Is. Victoria, Aus.

Genus *Pulvinites* Blainville, 1824

Type Species. *Pulvinites adansonii* Blainville, 1824, by monotypy.

Synonymy. *Hypotrema* d'Orbigny, 1853; *Foramulina* Hedley, 1914

Original diagnosis. 'Coquille mince, ovale, équivalve, subéquilatérale, à sommets bien marqués et à peine inclinés en avant; charnière composée par huit ou dix dents un peu divergents du sommet et séparées par autant de fossettes pour les ligamens; impressions musculaires inconnues' (Blainville 1824, p. 316).

Amended diagnosis. Pulvinitidae of medium size; not auriculate. RV flat or slightly concave, with scar of anterior byssal (pedal) retractor muscle displaced posteriorly by migration of foramen to occupy position just posterior to foramen's dorsal margin; scar of posterior retractor lies just ventral to this, off the foramen's ventro-posterior margin. LV weakly to strongly convex, with anterior byssal (pedal) retractor scar lying just beneath centre of ligamental area, just postero-dorsally of the apex of the posterior retractor scar (text-fig. 1).

Discussion. All previous accounts have credited DeFrance with authorship of both the genus and the type species. However, DeFrance's (1826*a, b*) entry in the Dictionnaire des Sciences Naturelle under the entry 'Pulvinite' was preceded by that of Blainville (1824) under 'Mollusca', and it is as a subcategory of this entry that the above diagnosis, albeit using the name '*Pulvinites Adansonii* DeFr.', was first given. Blainville's entry refers to the volume of plates of the same work which bears a publication date of 1826. However, even if this date is wrong and the relevant plate (pl. 88, fig. 3) had in fact already been published by the time that Blainville's entry was published, it can still not be regarded as a valid description since the plate caption uses only the vernacular name 'Pulvinite d'Adanson. (Def.)'. There is no doubt, therefore, that Blainville, 1824, is the true author of both genus and type species.

The type material has been destroyed and is represented only by rather poor photographs (Freneix 1956). Some of these, however, show muscle impressions and were presumably collected after the original diagnosis, in which it is stated that the scars were unknown, was written. The de Gerville collection topotypes in the British Museum (Natural History) clearly show muscle impressions and details of the foramen and suture. Blainville and DeFrance seem not to have been aware of these features.

The material from the upper Jurassic ('Corallien', now known to be of Kimmeridgian age—see Arkell 1956) of La Rochelle, for which d'Orbigny (1853) created the genus *Hypotrema*, was discovered in 1826 (d'Orbigny 1853) and seems first to have been referred to in the *Palaeontologie Française* (d'Orbigny 1847) under the name *P. oblonga* (*lapsus calami*). In the *Prodrôme* (d'Orbigny 1850), however, this species is not mentioned and the La Rochelle material is referred to *Pulvinites rupellensis*. Presumably the names *Pulvinites oblonga* and *Pulvinites rupellensis* applied to the same material. D'Orbigny subsequently, however (1853), noting that the foramen had not been mentioned in the original description of *P. adansonii*, decided that *Pulvinites* was no more than an ordinary *Perna* (= *Isognomon*) and that the genus was therefore invalid. It was for this reason that *Hypotrema* was erected, to encompass *Isognomon*-like forms which, like the La Rochelle material, truly had an enclosed foramen in the right valve. Since d'Orbigny's reasoning was erroneous, and since examination of de Gerville's collection or of Sowerby's (1833) plate would have proved the validity of *Pulvinites* Blainville, *Hypotrema* d'Orbigny, 1853, is an unequivocal synonym. This has been suspected by other workers (Bronn 1852; Deshayes 1864; Stoliczka 1871; Fischer 1886; Stephenson 1941; Vokes 1941; Freneix 1956). Cox (1969) re-defined *Hypotrema* and distinguished it from *Pulvinites* on three points: (i) *Hypotrema* is taller and narrower; (ii) in *Hypotrema* the byssal retractor and adductor scars touch in the left valve, and (iii) the ligamental area is arched in *Hypotrema* but straight in *Pulvinites*. Examination of a representative suite of material shows that valve profile is variable in both forms, and that the taller, narrower condition seen in some *Hypotrema* is not fully diagnostic and only of specific importance. Similarly, the ligamental area is variably straight or

arched in both forms. This leaves the relative position of the muscle scars in the left valve: in *P. mackerrowi* sp. nov., they touch in some specimens and not in others from the same population. None of these features is therefore likely to be of generic significance.

Foramelina Hedley, 1914 was erected for the newly discovered *F. exempla*. Hedley was aware of the similarity of his shell to both *Hypotrema* d'Orbigny, and to *P. argentus* Conrad, 1858. However, *Hypotrema* was rejected as a possible genus because of d'Orbigny's (erroneous) opinion that the foramen served for passage of a muscle, not a byssus as in Hedley's shell in which an uncalcified byssus was preserved. *P. argenteus* Conrad was stated to be assigned to that genus only with doubt (Hedley 1914, p. 71), and this gave him justification for establishment of his new genus. In fact, *F. exempla* is very similar to both *P. adansonii* and *P. argenteus*, differing principally in its larger size (length c.130 mm, cf. not more than 60 mm in the other two *Pulvinites*; see Table 1), and the corresponding larger number and wider spacing of the ligament pits (both of which increase during ontogeny). Apart from size, the details of musculature, profile, foramen, and suture are virtually identical in both forms and there is no doubt that they are congeneric species. Zinsmeister's (1978) reservations on inclusion of *Foramelina* in the Pulvinitidae, based on his perceived differences between the 'sub-umbonal orifice and groove' described in *Foramelina*, and the narrow suture of *Pulvinites*, are unwarranted. The two conditions are identical, and wholly different from that shown by the species which Zinsmeister calls *Melina percrassa* Tate (and which he considers a possible relative of *Foramelina*), in which the byssal slit, though deep, is both open to the anterior and located in the left valve.

All the species considered in this study are represented by at least some specimens whose muscle scars are well-enough preserved to indicate the points of insertion of the byssal (pedal) retraction muscles, as well as the adductor muscle, in both valves (text-fig. 1). These insertion points are in equivalent positions in each species, and their identity is confirmed by examination of the soft parts of *P. exempla*.

Pulvinites adansonii Blainville, 1824

Plate 72, fig. 1

- 1824 *Pulvinites Adansonii* Blainville, p. 316.
- 1826a *Pulvinites Adansonii* DeFrance, p. 107.
- 1826b Pulvinite d'Adanson DeFrance, pl. 88, fig. 3.
- 1833 *Pulvinites Adansonii* DeFrance; Sowerby, pl. 104.
- 1941 *Pulvinites auriculus* Vokes, p. 8, figs. 14, 15.
- 1956 *Pulvinites adansonii* DeFrance (partim.); Freneix, fig. A, 1-6.
- 1978 *Pulvinites antarctica* Zinsmeister, p. 567, pl. 1, figs. 1-4.

Types. Syntypes: DeFrance Coll., University of Caen, destroyed in 1944, figured by Freneix (1956), figs. 1-4. Topotypes: Gerville Coll. figured by Freneix (1956), figs. 5, 6 (incorporated with DeFrance Coll. and destroyed with them); Gerville Coll., British Museum (Natural History), BML 63618, 63619, 65685; British Museum (Natural History), BMLL 40007.

Original diagnosis. As for genus (Blainville 1824).

Emended diagnosis and description. Orbicular, or trigonal with a straight, slightly convex or slightly concave postero-dorsal shell margin. In adult, LV weakly inflated with length around 53 mm; length usually slightly greater than height; c.7-11 ligament pits on ligamental area of length c.6-11 mm; ratio of valve length to length of ligament greater than 4 (Table 1). Scars of adductor and byssal retractor muscles do not touch in LV; division of adductor scar into quick and catch portions is sometimes discernable.

Discussion. Sowerby's (1833) figure of topotypes (BML 63618, 61619) remains the best published illustration of this species, those of Freneix (1956) being of poor quality. Vokes' (1941) *P. auriculus* was distinguished from *P. adansonii* on the basis of its being 'more regularly rounded anteriorly and ventrally, and in being somewhat more produced posteriorly'. Presumably he only had DeFrance's

original figure to go on which is somewhat pointed anteriorly and not particularly produced posteriorly. In fact, Sowerby's (1833) figure shows the typical outline of *P. adansonii*, which is identical to that shown in Vokes' figures of *P. auriculus*. Zinsmeister (1978) did not consider the characteristics of *P. adansonii* when he erected his species *P. antarctica*. The holotype of his species has a slightly more orbicular outline than typical *adansonii* (not diagnostic), but the paratype is well within the limits of variation of that species.

Pulvinites argenteus Conrad, 1858

Plate 72, figs. 3, 4

1858 *Pulvinites argentea* Conrad, p. 330, pl. 34, fig. 5.

1956 *Pulvinites adansonii* DeFrance (partim.); Freneix.

Types. Conrad's types from Owl Creek, 4 km north-east of Ripley, Tippah Co., Mississippi are stated by Stephenson (1941) to be lost. He further states that specimens USNM 20667 and USNM 73635 in the National Museum in Washington (Smithsonian Institution) are good topotypes. A topotype (USNM 32741) is also illustrated (Pl. 72, figs. 3, 4).

Original diagnosis. 'Transversely subovate, compressed; perforated valve slightly concave; foramen oval, from its upper margin a channel extends to the apex; substance of shell silvery, thin; cardinal plate broad, with about thirteen radii or teeth; the lower valve presents within the appearance of two muscular impressions, the one above the other, the former striated' (Conrad 1858, p. 330).

Amended diagnosis. Orbicular, or trigonal with a straight, convex, or slightly concave postero-dorsal shell margin. In adult, LV weakly or moderately inflated with a length of around 53 mm; length equal to, slightly greater than, or slightly less than height; 10–15 ligament pits on a ligamental area of length c.9–15 mm; ratio of valve length to length of ligament less than 4 (Table 1). Scars of adductor and byssal retractor muscles do not touch in LV.

Discussion. Freneix (1956) wrongly regards this species as identical to *P. adansonii*. Although similar, the hinge plate is consistently broader for the equivalent valve length (Table 1) as was stated by Conrad in the original description. Conrad's original figure showed a particularly orbicular specimen; the more typical outline is the trigonal one figured by Wade (1926) and reproduced in Cox (1969).

Pulvinites rupellensis d'Orbigny, 1850

Plate 72, fig. 2

1847 *Pulvinitis oblonga* d'Orbigny; p. 522 (*nomen nudum*).

1850 *Pulvinites rupellensis* d'Orbigny; p. 24.

EXPLANATION OF PLATE 72

Pulvinites spp.: s = suture; f = byssal foramen; a = adductor muscle; apr = anterior pedal retractor; ppr = posterior pedal retractor.

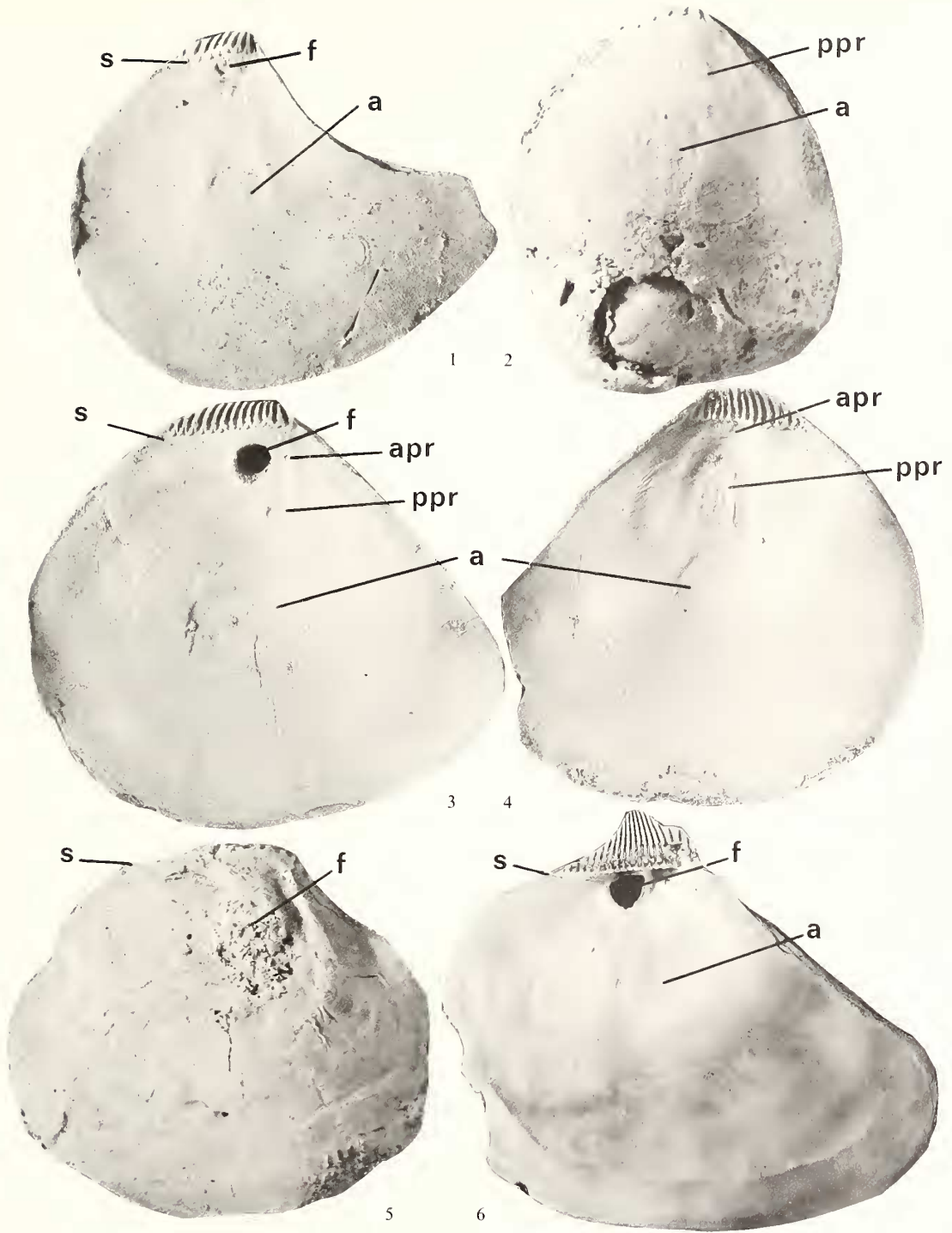
Fig. 1. *P. adansonii*, latex impression of mould of interior of right valve of topotype; Gerville Coll., British Museum (Natural History) BML 63618. $\times 1.3$.

Fig. 2. *P. rupellensis*, internal mould of left valve of topotype d'Orbigny Coll. Museum National d'Histoire Naturelle, I.P.M.—ORB 4314A. $\times 2.1$.

Figs. 3, 4. *P. argenteus*, internal views of right and left valves of hypotype; Ripley Formation, Coon Creek, Tennessee, USNM 32741. $\times 1.3$.

Fig. 5. *P. mackerrowi*, internal view of right valve from which the inner shell layer has been lost; holotype, $\times 2.7$. Wood Eaton quarry, nr. Oxford; Ardley Member of White Limestone Formation. Oxford University Museum J40183.

Fig. 6. *P. exempla*, internal view of right valve of paratype. Australian Museum, Sydney, C37004. $\times 0.5$.



PALMER, *Pulvinites*

- 1853 *Hypotrema rupellensis* d'Orbigny; p. 437, pl. 10, figs. 1–5.
 1853 *Hypotrema triangularis* d'Orbigny; p. 437, pl. 10, figs. 6–12.
 1929 *Hypotrema Rupellensis* d'Orbigny; Cottreau, pl. 20, figs. 17–19.
 1931 *Hypotrema Rupellensis* d'Orbigny; Cottreau, p. 1.

Types. Twenty-two specimens from d'Orbigny's collection are preserved in the Museum National d'Histoire Naturelle in Paris. These are now all labelled *H. rupellensis*, and come from La Rochelle (5 specimens, collective No. 4314) and Estré (17 specimens, collective No. 4314a). Estré is today a suburb of La Rochelle, called Aytré. The Paris specimens include those figured by d'Orbigny (1853) as *H. rupellensis*, and one of the figured syntypes of *H. triangularis* (labelled as *H. rupellensis*). The other figured syntypes of *H. triangularis* appear to be missing. Clearly, the material that d'Orbigny considered to constitute the second species has now been combined with that of the first. At the time of erection of the *nomen nudum*, *Pulvinitis oblonga*, d'Orbigny (1847) stated that he had only eight specimens. Whether this number constitutes the type suite of *Pulvinites rupellensis* d'Orbigny, 1850, and when the other specimens now in the d'Orbigny collection were added, are unknown. Other material from the La Rochelle region includes specimens nos. 255–258 in the collections of the Museum d'Histoire Naturelle at La Rochelle, and Oxford University Museum nos. JZ 1791–JZ 1801 from the coast at Marsilly just north of La Rochelle (author's collection). All specimens are of Kimmeridgian age.

Original diagnosis and description. 'Espèce remarquable, ovale ou oblongue, fixée sur le polypiers' (d'Orbigny 1850, p. 24).

Amended diagnosis and description. Orbicular, sub-trigonal, or, more commonly, dorso-ventrally elongated oval, with moderately or strongly inflated LV. Height in adult up to *c.*50 mm and usually much higher than long; 5–12 ligament pits on a ligamental area up to *c.*11 mm (Table 1). Adductor muscle scar in LV more dorsal than in Cretaceous species so that its dorsal edge is in contact with the ventral side of the main byssal retractor scar. Widely spread threadlike radial riblets on exterior of RV.

Discussion. The main component of growth in this species is in the ventral direction, rather than antero-posteriorly. The precise rate at which size increase in the anterior-posterior direction occurs is variable, so that some specimens are more or less symmetrically oval, whereas others have a more triangular profile like that of an egg. These latter specimens, with the shorter ligamental area (and thus less ligament pits), were separated into the species *triangularis* by d'Orbigny (1853) but in fact the range of variation is continuous. The most inflated specimens show the plane of the ligamental area rotated through 90° so that, as in *Anomia* with a similar lifestyle, the opening thrust of the ligament must have been dorsally directed.

Pulvinites mackerrowi sp. nov.

Plate 72 fig. 5; text-fig. 2

- 1969 *Nucula* sp.; McKerrow, Johnson and Jakobson, Table 8.
 1969 *Exogyra* sp.; McKerrow, Johnson and Jakobson, Table 8.
 1969 *Epithyrus oxonica* Arkell (partim.); McKerrow, Johnson and Jakobson, Tables 8, 9.

Types. (Oxford University Museum Collections); holotype: J43401; paratypes: J43402–J43486, J28030, J28035–J28038, J28041.

Derivation of name. After Dr. W. S. McKerrow, who first collected large populations of the species.

Diagnosis. Orbicular to (rarely) trigonally suboval, opisthogyrate with strongly inflated LV and well-developed umbo; approximately equidimensional, with length and height up to *c.*30 mm (Table 1). Outer shell surface smooth, or with xenomorphic ornament. Scars of adductor and byssal retractor muscles in LV may or may not touch; see Table 1 for measurements.

Discussion. This species is found in the Bathonian White Limestone Formation of Oxfordshire, where it occurs commonly in beds with a high proportion of corals and other epifauna (Palmer 1979). It is often found in life position on coral fronds or brachiopods; the xenomorphic ornament is one reason why it has been overlooked in the past. The combination of strong inflation, relatively small size, and the orbicular outline distinguish it from other species.